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1Evidence of social niche construction: persistent and repeated social
2interactions generate stronger personalities in a social spider

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13repeatability, *Stegodyphus mimosarum*

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17 While there are now a number of theoretical models predicting how
18 consistent individual differences in behaviour may be generated and
19 maintained, so far, there are few empirical tests. The social niche
20 specialization hypothesis predicts that repeated social interactions among
21 individuals may generate among-individual differences and reinforce within-
22 individual consistency through positive feedback mechanisms. Here we test
23 this hypothesis using groups of the social spider, *Stegodyphus mimosarum*,
24 that differ in their level of familiarity. In support of the social niche
25 specialization hypothesis, individuals in groups of spiders that were more
26 familiar with each other showed greater repeatable among-individual
27 variation in behaviour. Additionally, individuals that were more familiar with
28 each other exhibited lower within-individual variation in behaviour, providing
29 one of the first examples of how the social environment can influence
30 behavioural consistency. Our study demonstrates the potential for the social
31 environment to generate and reinforce consistent individual differences in
32 behaviour and provides a potentially general mechanism to explain this type
33 of behavioural variation in animals with stable social groups.

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INTRODUCTION

36

37 A fundamental goal in the field of the animal personality literature is to
38 understand the mechanisms responsible for generating and maintaining
39 consistent individual differences in behaviour. While there are now a number
40 of well-developed theoretical models predicting potential causal mechanisms
41 (reviewed in [1-3]), thus far empirical tests of these predictions are
42 extraordinarily few (but see [4-6]). In order to fully explain the presence of
43 consistent individual differences in behaviour, or personalities, a potential
44 mechanism would need to address the two key aspects of personality:
45 among-individual variation in behaviour and within-individual consistency
46 over time. A recent hypothesis termed the social niche specialization
47 hypothesis predicts that the social environment may play a key role in both
48 promoting individual differentiation and individual consistency [7, 8].

49 The social niche specialization hypothesis predicts that when a group
50 of individuals interacts repeatedly, it can be beneficial for them to develop
51 “social niches” [7, 8]. These social niches provide a way to reduce
52 competition among individuals and increase individual payoffs. First, by
53 differentiating their behaviour from each other individuals can reduce direct
54 competition with group mates [6, 9]. This type of niche specialization has
55 been well established in ecology, where the presence of competing
56 conspecifics can generate diet specializations among individuals [10, 11] and

57the social niche specialization hypothesis expands this concept beyond the
58foraging context. The presence of among-individual variation in behaviour
59can increase colony productivity [12] and individual reproduction [13] within
60social groups, supporting the prediction that social niches can enhance
61individual fitness and colony success.

62 Once among-individual differences in behaviour are established, the
63social niche specialization hypothesis predicts that they will be reinforced
64thereby generating within-individual consistency in behaviour [7, 8].
65Predictability in behaviour might increase successful interactions among
66individuals which can be especially important in stable social groups [1, 14].
67Within-individual consistency could also be generated if changing behaviour
68is too costly or if positive feedback mechanisms such as learning reinforce an
69individual's likelihood to repeat the behaviour [15, 16]. Therefore, the social
70niche specialization hypothesis addresses both aspects of animal personality
71by predicting that groups of individuals that have repeatedly interacted,
72should exhibit greater among-individual variation and lower within-individual
73variation in behaviour. Stated another way, familiar groups of individuals
74should exhibit stronger personalities.

75 While the development of social niches is theoretically possible in any
76group of repeatedly interacting individuals, these niches will likely be
77strongest when group membership is stable. When group turnover is low,
78individuals can more easily maintain the same social niche. For example,
79several studies have shown that individual birds will maintain consistent

80foraging behaviours when in the same social group [17, 18]. However, when
81the social context changes, frequently so will individual behaviour [17, 19].
82In particular, a recent study demonstrated that social interactions did not
83strengthen personalities in threespined sticklebacks, even when group
84membership was experimentally maintained [20]. However, in the wild,
85sticklebacks maintain fairly fluid groups with high turnover [21, 22].
86Therefore, it seems likely that social niche specialization holds the potential
87to be a more powerful mechanism in groups with stable membership where
88repeated interactions among individuals are frequent. Here we test the key
89prediction of the social niche specialization hypothesis that familiarity among
90group members should generate individual personalities using the social
91spider *Stegodyphus mimosarum*. Social spiders of the genus *Stegodyphus*
92offer a superb model to evaluate the social niche specialization hypothesis
93because the dispersal tendency of this species is extraordinarily low, and
94thus, persistent social interactions among colony members are a common
95feature in this species. Specifically, we compared the strength of consistent
96individual differences in behaviour in groups of spiders that had lived
97together for differing amounts of time, i.e. were more or less familiar with
98each other. We measured two ecologically relevant behaviours in this
99species: response to a simulated predator attack and response to a
100simulated prey encounter. Variation in these behaviours might influence task
101differentiation such as prey capture and colony defence as has been found in
102other species (e.g. [12, 23, 24]). If repeated social interactions generate

103social niches, we predicted that among-individual variation in behaviour
104would increase and within-individual variation would decrease with the
105amount of time the group had been together.

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METHODS

109

110Collection and Laboratory Maintenance

111 *Stegodyphus mimosarum* live in multi-female colonies ranging from 1-
1122000 members throughout eastern Africa [25, 26]. Their webs are composed
113of two structures: a two-dimensional capture web and a dense three-
114dimensional retreat composed of a series of silken tunnels. Spiders reside
115within their retreat for the majority of the day, and only emerge in response
116to prey or at night in order to repair their capture web. Females cooperate
117together in colony maintenance tasks including collective web maintenance
118and defence, cooperative prey capture, and alloparental care [27]

119 Ten colonies of *S. mimosarum* were collected in the town of Bela-Bela
120(24°53'S 28°17'E) in Limpopo, South Africa in November 2012. Colonies were
121collected by knocking down their capture webs, trimming off colonies'
122supporting foliage, and placing the colony in a cloth pillow case. Colonies
123were then transported to laboratory at the University of Pittsburgh, USA.
124Colonies were sorted in laboratory and their colony size (1-700 spiders) was
125determined. Eight of the largest colonies (400-600 individuals) were selected

for use in our study. From each of these colonies we haphazardly selected 48 females for inclusion in our studies. Assignment of females to different treatments groups was determined randomly using a random number generator in Excel (Microsoft 2010). Prior to being assigned to a treatment, females were housed individually in 2-oz deli cups that contained a dome of poultry wiring to facilitate web construction. Females were maintained in isolation for four weeks prior to the start of our experiment and sustained on an *ad libitum* diet of size-matched two-week old crickets.

134

135

136 **Manipulation of Familiarity**

137 In order to observe how repeated social interactions influenced among-
138 and within-individual behavioural variation, we manipulated the amount of
139 time groups of spiders lived together. We generated 64 experimental
140 colonies of 6 individuals and each colony was assigned to one of two
141 familiarity treatments: control colonies (N=32 colonies) where familiarity was
142 maintained throughout the experiment, and mixed colonies where familiarity
143 changed over the experiment. Altogether the familiarity treatment ran for
144 five weeks, and within each treatment, each colony was exposed to a social
145 disturbance after either one, two, three or four weeks (N=8 groups per social
146 disturbance per treatment). So for example, colonies that experienced a
147 social disturbance after one week were then left undisturbed for four weeks
148 and would have longer to become familiar with each other than colonies that

149were disturbed after four weeks. By varying the time of the social
150disturbance we could investigate how the length of social familiarity
151influenced individual behavioural variation. The social disturbance involved
152all of the members being removed from the colony and then being placed
153into a new container with all the same individuals (control treatment), or with
154new and unfamiliar individuals (mixed treatment). Colonies in the mixed
155treatment were reassembled using individuals from the same source colony
156that had not previously interacted. Therefore, individuals in the control and
157mixed colonies both experienced the same disturbance, but only the identity
158of the individuals in the mixed colonies was altered; any differences between
159the control and mixed colonies we could attribute to differences in familiarity
160among colony members.

161 We used a split-design where each of our eight source colonies were
162used to establish one replicate of each of our eight treatment combinations
163(mixed and control colonies at one, two, three and four weeks since social
164disturbance). Relatedness among individuals is known to influence social
165spider behaviour [28, 29] and this design ensured that all source colonies
166equally contributed to all treatment groups. Therefore, if relatedness among
167individuals was more influential on behaviour than familiarity, we would
168expect to see no differences between the control and mixed colonies. All
169experimental colonies were housed in 1.5L clear, plastic deli cups which
170contained a concave-up dome of poultry wiring to facilitate web construction.
171Lids were covered with a 1mm x 1mm screen which allowed ample airflow

172and low humidity levels. Colonies were kept on a maintenance diet of *ad*
173*libitum* six-week old crickets once weekly. To ensure successful prey capture,
174crickets were immobilized prior to being place in colonies' capture webs.
175After the social disturbance, all individuals were rehoused within a new 1.5L
176container with chicken wire. All colonies resumed normal feeding behaviour
177within three days of the social disturbance. At the end of our five week
178experiment, all colonies were disassembled, individuals were isolated back
179into 2-oz deli cups, and their personality types were repeatedly assayed daily
180for the next ten days in two ecological contexts.

181

182**Personality Assay: Boldness towards Predators**

183 This assay was designed to measure how quickly an individual
184recovered from a potential predator attack. Variation among individuals in
185this behaviour could be influential in determining individual specializations
186within the nest on tasks such as colony defence [12, 23, 24] and is a known
187determinant of division of labour and collective behaviour in this species.
188Boldness-shyness assays were initiated by removing spiders from their home
189containers and placing them within a rectangular enclosure (13.5 cm x 13
190cm x 3.5 cm). Spiders were permitted 60 sec to acclimate before applying
191two rapid jets of air to the dorsal, anterior part of the animal from
192approximately 10 cm away, using an infant ear-cleaning bulb. This stimulus
193universally elicited a huddle response from *S. mimosarum*, and resembles
194the rapid approach of an avian predator [23, 30]. As our measure of

195boldness, we recorded the individual's latency to resume movement
196following the huddle response. Five boldness assays (one per day) were
197completed on each spider beginning 24 hours after the end of the familiarity
198treatments. After completing their assays spiders were returned to their
199home containers.

200

201**Personality Assay: Tendency to Attack Prey**

202 This assay was designed to measure how quickly an individual
203attacked a simulated prey item; a behaviour that is likely important in
204determining foraging task specializations within a colony [12, 23, 24]. We
205staged prey capture events in spiders' home containers and noted whether
206they attacked a prey stimulus or not. Using a simulated prey item allowed us
207to standardize the prey escape cues each spider was exposed to. Trials were
208initiated by removing the lid to spider's container and placing a 1.5 cm x 1.5
209cm piece of printer paper in the spider's capture web. We then provided
210spiders 2 minutes acclimation time before administering a vibratory
211stimulus. We subsequently vibrated the paper using a portable, handheld
212vibratory device (FunFactory, Minivibe Bubbles). A thin aluminium wire
213extended from the end of the vibrator and made contact with the paper,
214which resulting in the paper fluttering back and forth within the capture web
215similar to Lepidopteran prey. We vibrated the paper for a total of ten
216minutes, or until the spiders emerged and bit the paper. For this behavioural
217assay we recorded a binary response of whether the spider approached and

218attacked the stimulus within the ten minute timeframe or not. . Prey capture
219assays started 24h after individuals had completed their boldness assays.
220This ensured that individuals had enough time to construct rudimentary
221capture webs and retreats within their home containers. Prey capture assays
222were implemented daily for five days.

223

224

225**Data analysis**

226 In order to ease analysis and interpretation of our data, we first
227inverted our measure of boldness: latency to resume movement after a
228huddle response. To do this, we subtracted each individual's latency from
229the maximum time of ten minutes (600 seconds). Therefore, individuals with
230higher boldness scores were considered more "bold," i.e. they resumed
231movement more quickly after the huddle response, compared to individuals
232with lower boldness scores which were considered more "shy". The resulting
233boldness scores were non-Gaussian distributed and best approximated a
234Poisson error distribution which we used for all further analyses. Attack
235tendency was a binary variable and we used a categorical (yes/no) error
236distribution for all analyses.

237 We first tested for the main effects of familiarity treatment (mixed
238versus control) and time since social disturbance (one, two, three, four
239weeks) on each of our behavioural measures. We ran a separate generalized
240linear mixed model for each behaviour including familiarity treatment, time

241since social disturbance and their interaction as fixed effects. We also
242included individual, experimental colony and source colony as random
243effects to account for the non-independence of our behavioural measures.
244There was no significant variation among experimental or source colonies
245and so we subsequently removed these effects from further analyses.

246 Our primary research question was to determine whether increasing
247familiarity among colony mates increased consistent individual differences in
248behaviour. To test this we compared the among- and within-individual
249variation components of each behaviour in each of our treatment
250combinations. However, it is important to note that because of its binary
251nature, it is impossible to directly estimate the within-individual (residual)
252variance in attack tendency. We ran a separate model for each behaviour in
253each familiarity treatment (control versus mixed) at each time point (weeks
254since social disturbance) including individual as a random effect. We then
255used these variance components to estimate repeatability as the proportion
256of total variation attributable to among-individual variation. We corrected all
257repeatability estimates as appropriate for each behaviour's distribution
258(Poisson with additive overdispersion for boldness, binary for attack
259tendency; [31]). We did not include any other fixed or random effects, such
260as experimental colony, source colony or body size, as these factors only
261varied between, not within, individuals and any variance attributable to
262these factors would remain in the within-individual (residual) variance
263providing a conservative repeatability estimate [32]. Additionally, in

preliminary analyses we found that these effects had no significant or consistent effect on either behaviour nor accounted for any significant portion of behavioural variation (data not shown). Therefore all repeatability estimates reported here can be considered “non-adjusted” and should be more broadly generalizable [31]. We used generalized linear mixed models with Markov Chain Monte Carlo estimation for all analyses. MCMC is a Bayesian statistical method that is powerful for fitting non-Gaussian distributions and partitioning variance among random effects [32, 33]. We used MCMCglmm [33] in R 2.15 (<http://www.r-project.org/>) which returns 95% credibility intervals for both fixed and random effects. If the 95% CI’s of two variance estimates did not overlap, we interpreted this as evidence that the estimates are significantly different from each other. Throughout we used non-informative proper priors [33] appropriate for the relative error distributions (Poisson for boldness; categorical for attack latency) and preliminary analyses indicated that our results were not sensitive to changes in prior settings (data not shown). We ensured convergence and adequate chain mixing by comparing the posterior distributions and auto-correlation plots of five independent chains with 500,000 iterations, a 1,000 burn-in period and thinning every 100 iterations for each model.

283

284

RESULTS

285

286 The average boldness score across all individuals was 216 ± 5.3 (\pm
287stn. error), meaning that individuals resumed moving after the huddle
288response after 383 seconds. While there was no main effect of familiarity
289treatment (treatment effect: -0.97, 95% CI: [-2.99, 1.16]) there was a
290significant effect of time since social disturbance (time effect: -0.56 [-1.16, -
2910.03]). Groups that had been together longer tended to be shyer than
292groups that had recently been disturbed (Figure 1a). This effect did not
293differ between the two colony types (colony x time interaction: -0.31 [-0.56,
2941.02]).

295 Across both treatments and all time periods, attacks on a simulated
296prey item occurred in 25% of all trials This proportion did not differ between
297colony types (colony effect: -0.008 [-1.13, 1.25]) or across time (time effect: -
2980.11 [-0.42, 0.22]; colony x time interaction: 0.15 [-0.30, 0.58]; Figure 1b).

299 We found evidence for consistent individual differences in both
300boldness and attack tendency in both familiarity treatments (Figure 2, Table
3011). In support of the social niche specialization hypothesis, the repeatability
302of boldness was significantly higher in the control colonies compared to the
303mixed colonies at all time points, except when the colonies had not been
304disturbed for four weeks. Importantly, this increase in repeatability was
305driven by lower within-individual variation in boldness in the control colonies
306compared to the mixed colonies. This means that individuals in the control
307colonies exhibited more consistent behaviour at all time points compared to
308individuals in the mixed colonies. Additionally, the among-individual

309variation and therefore repeatability of boldness significantly increased the
310longer a group had been together regardless of whether it was a control or
311mixed colony. After not being disturbed for four weeks, individuals in the
312mixed colonies achieved similar among- and within-individual variation as
313those in the control colonies. In contrast, the repeatability of attack
314tendency remained at a similar level in both familiarity treatments across all
315time periods (Table 1)

316

317

DISCUSSION

318

319 The field of animal personality currently seeks potentially generalizable
320mechanisms that can generate and maintain consistent individual
321differences in behaviour. The social niche specialization hypothesis offers
322one such mechanism. The social niche specialization hypothesis posits that
323individuals will develop social niches as a result of living within a stable
324social group. In support of this view, we demonstrated here that consistent
325individual differences in boldness behaviour increased in the social spider *S.*
326*mimosarum* the longer that individuals remained in a stable social group.

327

328 We recovered evidence that social niches for boldness behaviour
329developed as a result of familiarity among colony mates. Control colonies all
330experienced a social disturbance but were placed back with their original
331familiar colony mates. If social group familiarity is a key driver of
332repeatability, we would expect to see stronger personalities in these

332 individuals as compared to the mixed colonies, regardless of when the social
333 disturbance occurred. As predicted, the repeatability estimates of boldness
334 were significantly higher in the control colonies than mixed colonies at all
335 time points, except when the colonies had not been disturbed for four weeks.
336 This increase in repeatability was driven by lower within-individual variation
337 in the control colonies. Individuals became more consistent in their
338 behaviour the longer they had spent with a social group, supporting the
339 hypothesis that repeated social interactions can increase the benefits of
340 predictable behaviour [7, 8]. Our data suggest that, at least in this species,
341 four weeks of repeated social interactions are needed to fully establish social
342 niches. While several studies have now investigated how different ecological
343 factors influence among-individual variation in behaviour [4-6, 11], fewer
344 have investigated how these factors generate individual consistency in
345 behaviour (but see [19, 34]). Our study demonstrates that the stability of
346 the social environment may be especially influential in generating and even
347 reinforcing individual differences once they appear. A promising next step
348 will be to test whether colonies composed of behaviourally consistent
349 (predictable) members perform better than colonies of unpredictable
350 individuals.

351 While we found evidence for increased social niches in boldness with
352 longer group fidelity, we found no such pattern for individuals' tendency to
353 attack. Repeatabilities in attack tendency were similar regardless of the
354 familiarity treatment or the time since the social disturbance. The overall

low attack rates (attacks only occurred in ~25% of all trials) and distribution of the data (it is impossible to directly estimate the within-individual variance in a binary variable) likely reduced our ability to partition the behavioural variance. Granted, it is possible that our simulated prey was not as realistic as we hoped; however, this interpretation is at odds with the findings of other studies on other social *Stegodyphus* that used identical methods [23]. Another explanation may be that attack tendency is more strongly influenced by genetic or un- (or slowly-) changing state variables, such as body size [35, 36]. While we found no evidence that body size influenced attack tendency in *S. mimosarum* (data not shown), it remains that some other unmeasured state variable may influence this particular behaviour. It is also possible that among-individual variation in this particular behaviour is not as important as variation in boldness in familiar groups; other studies have found relatedness to be the most influential determinant of foraging efficiency in some social spiders [28, 29]. Consistent with this view, [12] found that colony productivity increased with within-colony variation in some aspects of behaviour (brood care and exploration) but not others (aggressiveness). Boldness has already been implicated as an important determinant of task differentiation in other *Stegodyphus* species [23, 24] and our data support the finding that among-individual differences in boldness are a particularly important element of social organization in social *Stegodyphus*.

377 Social niche specialization may be a particularly powerful mechanism
378for generating social organization in societies where individuals exhibit group
379fidelity, such as our spiders. In contrast, it may be difficult for evolutionary
380processes to select for the proper mix of personalities in groups where
381membership changes with each generation. This may help to explain why a
382previous study on sticklebacks recovered no evidence that repeated social
383interactions increased among-individual variation or within-individual
384consistency in behaviour [20]. Because, sticklebacks form large schools in
385the wild, and while certain pairs are found together more often than chance
386would predict [21], school membership is generally fluid [21, 22]. We argue
387that in these types of groups, the formation of social niches will be difficult
388since individuals are constantly interacting with new individuals (e.g. [37]).
389Instead we expect that more plastic behaviour would be beneficial. In
390contrast, repeated social interactions in more stable societies may provide a
391mechanism by which individual sense gaps in their societies' workforce and
392fill them, i.e., via shifts in personality. In other words, simple mechanisms
393such as positive feedback loops throughout development may, over time,
394permit the adaptive differentiation of individuals' personalities and (perhaps)
395their social roles. Such simple feedback loops have been implicated in
396numerous studies on social insect societies and manifest behaviourally as
397individual differences in task performance thresholds ([38, 39]but see [40]).
398Here we studied how repeated social interactions among individuals in a
399social group influences behavioural variation, but another potential scenario

400where social niches might be important is in species with long-term mating
401partnerships [14]. An exciting area for future research would be to
402investigate how the number of stable social partners influences the
403development of social niches.

404

405**Conclusions**

406 The presence of consistent individual differences in behaviour have
407sparked so much interest in part because they have the potential to impact
408any number of evolutionary and ecological processes. And, while studies
409documenting the presence of personalities in animals continue to grow, we
410still know little about the factors responsible for their existence. Here we
411show that living in stable social groups has the potential to generate and
412maintain consistent individual differences in behaviour. Individuals that were
413from groups that were more familiar with each other exhibited greater
414among-individual variation and within-individual consistency in behaviour.
415Many species form social groups, suggesting that the development of social
416niches may allow individuals to increase their own fitness by enhancing their
417fit with their (social) environment. However, stability of group membership
418can vary dramatically among species and populations and we urge that more
419studies explore the potency of group fidelity to drive the generation and
420maintenance of individual differences in key functional traits, such as
421behaviour.

422

423

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Table 1. Variance component (among- and within-individual) and repeatability estimates of boldness and attack behaviours in control and mixed colonies that experienced a social disturbance one, two, three, or four weeks ago. The within-individual variance could not be estimated for the binary variable of attack tendency (see methods for details). Numbers in [] indicate 95% credibility intervals.

		Time since social disturbance			
		One week	Two weeks	Three weeks	Four weeks
<i>Boldness</i>					
Control colonies					
Among	6.87 [3.94, 11.49]	21.80 [11.90, 36.32]	15.11 [9.12, 29.53]	23.41 [13.03, 46.33]	
Within	4.45 [3.51, 6.06]	3.52 [2.64, 4.79]	2.61 [2.00, 3.64]	4.95 [3.61, 7.22]	
R	0.62 [0.47, 0.73]	0.86 [0.78, 0.92]	0.86 [0.79, 0.93]	0.83 [0.73, 0.91]	
Mixed colonies					
Among	4.12 [0.78, 10.30]	0.05 [0, 7.05]	11.93 [6.24, 21.52]	21.75 [11.22, 42.17]	
Within	19.31 [14.47, 27.03]	23.58 [16.68, 33.20]	12.01 [8.82, 16.33]	9.91 [7.12, 13.69]	
R	0.16 [0.05, 0.36]	0.002 [0, 0.24]	0.54 [0.35, 0.66]	0.74 [0.56, 0.82]	
<i>Attack tendency</i>					
Control colonies					
Among	1.40 [0.39, 4.85]	1.73 [0.32, 5.00]	6.26 [2.16, 18.37]	2.02 [0.21, 6.24]	
R	0.32 [0.12, 0.56]	0.35 [0.12, 0.56]	0.70 [0.42, 0.85]	0.32 [0.11, 0.62]	
Mixed colonies					
Among	2.88 [0.84, 7.45]	3.14 [0.94, 8.73]	4.30 [1.46, 13.15]	3.31 [1.23, 8.68]	
R	0.45 [0.22, 0.66]	0.50 [0.23, 0.70]	0.55 [0.34, 0.78]	0.50 [0.26, 0.70]	

FIGURE LEGENDS

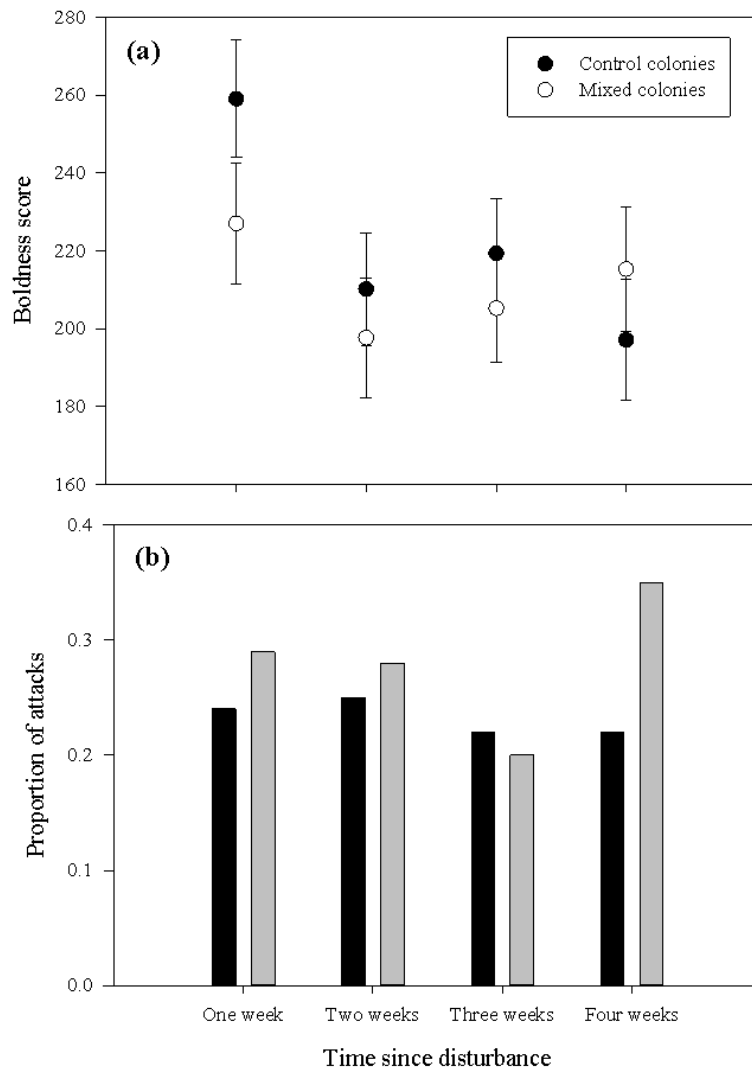
613**Figure 1.** Average (\pm stn. error) boldness scores (a.) and proportion of prey
614attacks (b.) in the mixed and control colonies that experienced a social
615disturbance one, two, three, or four weeks ago.

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617**Figure 2.** Among-individual (a.), within-individual (b.), and the resulting
618repeatability estimate (c.) in boldness scores in the mixed and control
619colonies that experienced a social disturbance one, two, three or four weeks
620ago. Error bars represent the 95% CI for each estimate.

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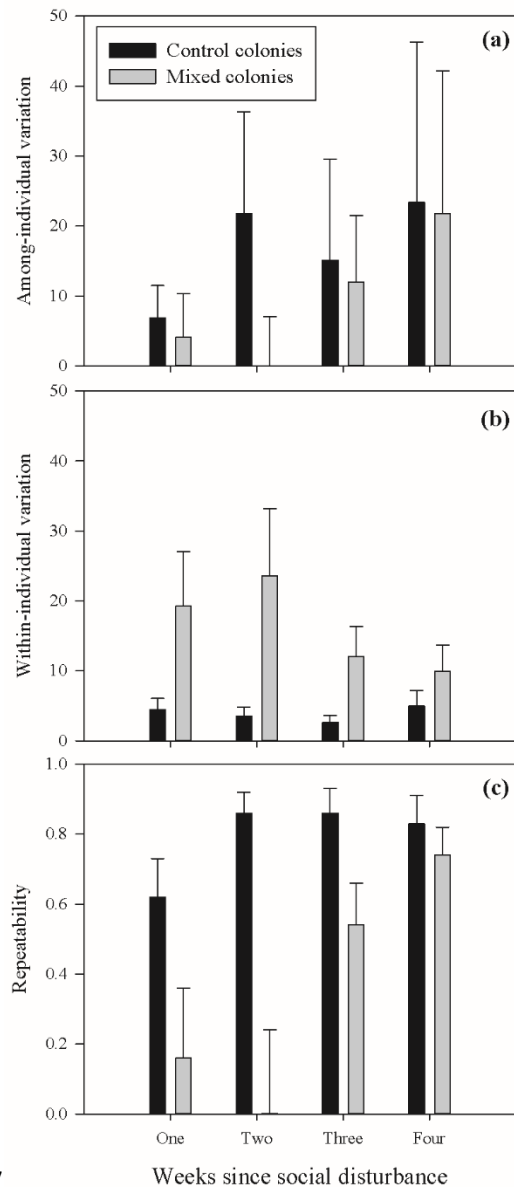


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624**Figure 1.**

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628 **Figure 2.**
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